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Partial Dominance, Pleiotropism, and Epistasis in the Inheritance of the High-Oleate Trait in Peanut

T. G. Isleib,* R. F. Wilson, and W. P. Novitzky

ABSTRACT

Earlier reports of the high-oleate (low-linoleate) trait in peanut (*Arachis hypogaea* L.) indicated that it was controlled by completely dominant gene action. However, linoleate content intermediate to that in low- and normal-linoleate seeds was found among progeny when the trait was backcrossed into five virginia-type cultivars, suggesting partial dominance of the gene controlling the trait. Although BC_1F_2 results were inconsistent across recurrent parents, data from the BC_2F_2 and BC_3F_2 populations of all crosses conformed to the 1:2:1 ratio expected under partial dominance. Quantitative analysis showed that fatty acid levels were affected by the background genotypes of the recurrent parents, suggesting that there are other genes that influence fatty acid. The *ol* gene exhibited pleiotropism by influencing not only oleate and linoleate, but also levels of palmitate, total C_{18} fatty acids, gadoleate, and total saturated fatty acids. The effects of the *ol* gene interacted with background genotype, particularly with the additive genetic contrast, suggesting epistasis in the general sense. Progeny testing of 59 putatively heterozygous and 41 homozygous normal BC_2F_2 plants indicated that the two genotypes could be distinguished accurately on the basis of linoleate level, suggesting that the *ol* gene can be moved by backcrossing using techniques appropriate for a dominant trait rather than a recessive trait.

THE HIGH-OLEATE TRAIT (low-linoleate) of peanut results in longer shelf-life for peanuts and peanut products and is therefore of great interest to the U.S. peanut industry (Ahmed and Young, 1982). In most U.S. germplasm, the trait is controlled by two duplicate genes, ol_1 and ol_2 (Moore and Knauft, 1989), one of which is common in U.S. runner- and virginia-type peanut cultivars as evidenced by the high frequency of monogenic segregation ratios observed in crosses of these types of cultivars with F435, the source of the trait (Knauft et al., 1993; Isleib et al., 1996). Earlier reports of the high-oleate trait indicated that the rare gene controlling the trait (hereafter called *ol*) exhibited complete recessivity (Moore and Knauft, 1989; Knauft et al., 1993; Isleib et al., 1996). Different patterns of inheritance indicative of three-gene control with dominant and recessive epistasis were detected in crosses of F435 with parents of the spanish market type (López et al., 2001, 2002). This work also suggested quantitative inheritance beyond the genes with large influence on the trait.

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The peanut breeding program at N.C. State University (NCSU) among others has been backcrossing the high-oleate trait into several different cultivars and breeding lines. At NCSU, the initial cycle of selection followed several generations of single-seed descent designed to increase the probability of recovering high-oleate plants from populations of limited size. The fatty acid assay used in the first cycle required that oil be extracted from a sample of several seeds (Isleib et al., 1996). Subsequent cycles of backcrossing and selection have been based on data collected from small cotyledonary samples from individual F_2 seeds as described by Zeile et al. (1993). In the three cycles of backcrossing completed since the initial cycle of selection, it was observed that although the high-oleate/low-linoleate seeds were readily identified by having linoleate values below 70 g kg^{-1} of total fatty acids, there was a broad range of values for linoleate and oleate in the non–high-oleic "normal" plants. The objectives of this study were to determine whether the distributions of fatty acid contents conformed to simple dominance, to quantify the effect of the rare *ol* gene on oleate, linoleate, and other fatty acids, and to determine whether the effect of the *ol* gene was uniform across background genotypes.

MATERIALS AND METHODS

The initial crosses of large-seeded virginia-type cultivars NC 7 (Wynne et al., 1979), NC 9 (Wynne et al., 1986), NC 10C (Wynne et al., 1991a), NC-V 11 (Wynne et al., 1991b), and VA-C 92R (Mozingo et al., 1994) to F435 were made in 1990 as described by Isleib et al. (1996). The first backcross to each of the five cultivars was made in the summer of 1994 using $F_{4:5}$ lines identified with the high-oleate trait as nonrecurrent parents. BC_1F_1 plants were grown in the greenhouse during the winter of 1994–1995. BC_1F_2 seeds were harvested and analyzed for fatty acid content as described by Zeile et al. (1993). A plug of cotyledonary tissue was removed from the seed by inserting a sharpened ball inflator needle into the seed perpendicular to the plane of the lumen. The plug was placed in a vial. The lipids in the plug was extracted for 8 h in 0.5 mL of chloroform/hexanes/methanol (8:5:2, V/V/V). Fatty acid methyl ester derivatives were made by transesterification using sodium methoxide. Fatty acids were quantified using an HP 5890 Series II GC equipped with dual AT-Silar (Alltech Assocs., Deerfield, IL) columns (30 m by 0.53 mm i.d.) and flame ionization detectors (FIDs). The carrier (He) flow was 5 mL min^{-1}, temperatures were 250°C for the injectors, 200°C for the oven, and 275°C for the FIDs. Retention times and response factors for the eight peaks of interest were calibrated against authentic standards (Supelco, Bellefonte, PA). In addition to the concentrations of individual fatty acids, sums were computed for total C_{18} fatty acids, that is, the total of the concentrations of stearate, oleate, and linoleate; the total satu-

Abbreviations: O/L ratio, ratio of the concentration of oleate to linoleate.

rated fatty acids (the total of the concentrations of palmitate, stearate, arachidate, behenate, and lignocerate), and the ratio of the concentration of oleate to that of linoleate (O/L ratio). The same protocol was used to produce and assay the BC_2F_2 and BC_3F_2 populations in subsequent years.

Linoleate content was used as the criterion for identifying seeds expressing the high-oleate trait. Seeds with linoleate content less than 70 g kg^{-1} were considered to be homozygous recessive for the ol_1 and ol_2 genes. This process was repeated in each of the two following years, each time selecting seeds with linoleate content less than 70 g kg^{-1} for use as parents in the subsequent cycle of backcrossing, selfing, and selection. When several such seeds were found in the progeny of a single BC_1F_1 plant, the seed with the lowest concentration of total saturated fatty acids was selected for use as parent of the next generation in that particular line of backcrossing.

Linoleate contents of BC_1F_2 seeds derived from a given recurrent parent were sorted from lowest to highest and plotted in column graphs to permit visual inspection of the distributions. The graphs were examined for discontinuities in the progression of linoleate values. The first break point in each distribution was always near 70 g kg^{-1} linoleate, and seeds with linoleate contents less than the first break point in the distribution were classified as *olol* homozygotes. Seeds with linoleate contents between the first and second break points were classified as *Olol* heterozygotes, and those above the second break point were classified as *OlOl* homozygotes. Chi square analyses were performed to determine if the observed distributions

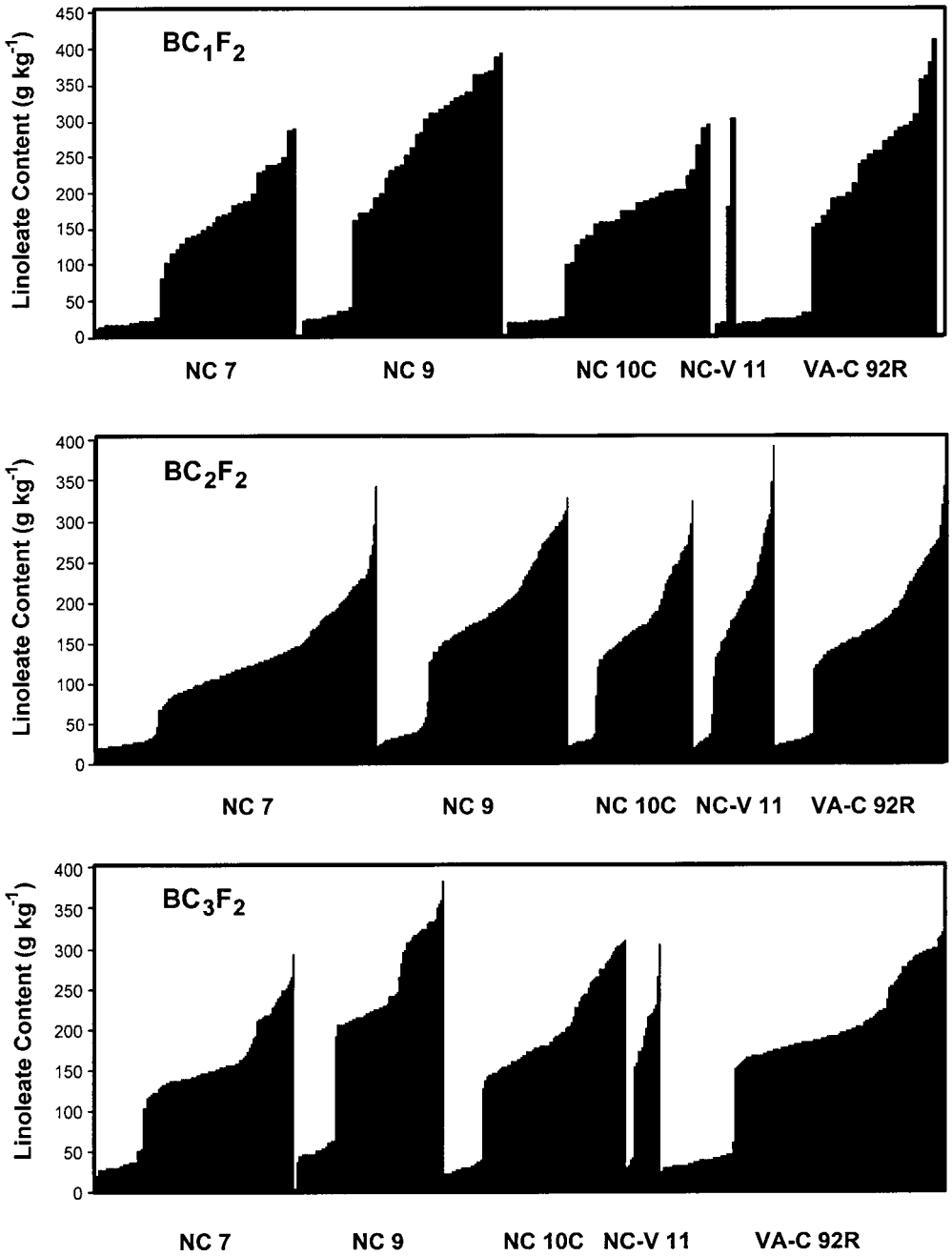

Fig. 1. Distribution of linoleate content in BC_1F_2, BC_2F_2, and BC_3F_2 populations using five recurrent parents. Each bar represents linoleate content in a single seed.

conformed to the expected 1:2:1 Mendelian ratios. Analysis of variance was performed to determine the significance of genotypic effects. The sums of squares for *ol* genotype and genotype × recurrent parent interaction were divided into parts due to the additive contrast, a = (G_{olol} − G_{OlOl})/2, and dominance contrast d = G_{Olol} − (G_{OlOl} + G_{olol})/2, where G refers to the genotypic value associated with the genotype indicated by the subscript. Least squares means were estimated for each *ol* genotype in each genetic background and for the *ol* genotypes averaged across all five genetic backgrounds in the BC_3F_2. Additive and dominance contrasts were likewise estimated for each background genotype and across all background genotypes.

To confirm the predictive value of the linoleate content of individual seeds as an indicator of the *ol* genotype, progeny tests were conducted for 100 BC_2F_2 seeds representing backcrosses to all five recurrent parents: 59 putative heterozygotes and 41 putative normal homozygotes. Each seed was planted in the field in 1997, grown to maturity, and its seed harvested separately. Ten seeds were tested initially for each plant progeny. When the progeny segregated for dominant and recessive phenotypes, the plant was concluded to be heterozygous. When no recessive phenotypes appeared among the first 10 seeds, an additional 10 seeds were tested. If there were no recessive phenotypes among the 20 progeny, the plant was concluded to have been *OlOl*. With monogenic inheritance of the trait in a population, the probability that a nonrecessive BC_iF_2 seed is heterozygous is 2/3 and homozygous *OlOl* 1/3, and the conditional probability of finding no *olol* seeds among n given that the parent plant was *Olol* is $(0.75)^n$. By application of Bayes rule, the probability that a plant was *OlOl* given that it produced *n Ol-* seeds is $1/[1+(0.75)^n]$ or approximately 0.899 for $n = 10$ and 0.994 for $n = 20$. Chi square tests with the Yates correction were used to compare the observed incidence of heterozygotes and normal homozygotes with the 2:1 ratio expected with the expected if putative identification of the genotype occurred at random.

RESULTS AND DISCUSSION

The distributions of linoleate content in the BC_1F_2 generation for the five recurrent parents showed clear separation of seeds with low linoleate (high oleate) from those with high linoleate (Fig. 1a). When linoleate contents were sorted from lowest to highest, some populations exhibited apparent "break points" or "shoulders" in the distributions that might indicate differences between heterozygotes and dominant homozygotes (Fig. 1). These break points occurred at different linoleate levels in different populations. Chi square testing showed that the distributions in the populations derived from NC 7 and VA-C 92R were inconsistent with the 1:2:1 ratio expected (Table 1) while the populations derived from NC 9, NC 10C, and NC-V 11 fit the expected numbers relatively well. In the BC_2F_2 generation, there were substantially more individual seeds analyzed and the shoulders in the populations' distributions were more readily detected (Fig. 1b). All five populations conformed to the 1:2:1 ratio in contrast to the data reported in Isleib et al. (1996) in which it was concluded that NC-V 11 carried dominant alleles at both the ol_1 and ol_2 loci. The larger numbers of F_2 seeds analyzed in the current study suggest that all five recurrent parents carry one of the recessive *ol* alleles and are thus either $Ol_1Ol_1ol_2ol_2$ or $ol_1ol_1Ol_2Ol_2$. Similar patterns were observed in the BC_3F_2 generation (Fig. 1c, Table 1).

Quantitative analysis of the fatty acid concentrations in the BC_3F_2 population led to several conclusions about the inheritance of the high-oleate trait. First, it is apparent that there are other genes that influence fatty acid concentration (Table 2). The five backcross populations varied ($P < 0.01$) in the average concentrations of all individual fatty acids as well as the O/L ratio. Only total saturates did not vary with population on average. Continuous variation for fatty acid concentrations among peanut genotypes has been well documented (Khan et al., 1974; Tai and Young, 1975; Norden et al., 1987; Mercer et al., 1990; López et al., 2001, 2002), and until the discovery of the high-oleate trait and the elucidation of its genetic control, this variation was thought to be

Table 1. Segregation ratios observed for linoleate content measured in single seeds in the BC_1F_2, BC_2F_2, and BC_3F_2 generations in backcrossing the high-oleate trait into five virginia-type cultivars.

		Observed					
Generation	Recurrent parent	Low	Medium	High	χ^2 test	df	Probability
BC_1F_2	NC 7	19	19	5	9.628	2	$0.005 < P < 0.01$
	NC 9	10	24	6	2.400	2	$0.25 < P < 0.50$
	NC 10C	11	24	5	3.400	2	$0.25 < P < 0.50$
	NC-V 11	2	1	1	1.500	2	$0.25 < P < 0.50$
	VA-C 92R	15	21	4	6.150	2	$0.025 < P < 0.05$
	Total				23.148	10	$0.01 < P < 0.025$
	Pooled	57	89	21	16.246	2	$P < 0.005$
	Heterogeneity				6.902	8	$0.50 < P < 0.75$
BC_2F_2	NC 7	112	268	110	4.335	2	$0.10 < P < 0.25$
	NC 9	91	167	82	0.582	2	$0.50 < P < 0.75$
	NC 10C	50	112	58	0.655	2	$0.50 < P < 0.75$
	NC-V 11	36	78	26	3.257	2	$0.10 < P < 0.25$
	VA-C 92R	71	159	70	1.087	2	$0.50 < P < 0.75$
	Total				9.915	10	$0.25 < P < 0.50$
	Pooled	360	784	346	4.346	2	$0.10 < P < 0.25$
	Heterogeneity				5.569	8	$0.50 < P < 0.75$
BC_3F_2	NC 7	29	68	23	2.733	2	$0.25 < P < 0.50$
	NC 9	24	39	27	1.800	2	$0.10 < P < 0.25$
	NC 10C	23	56	31	1.200	2	$0.50 < P < 0.75$
	NC-V 11	4	14	2	3.600	2	$0.10 < P < 0.25$
	VA-C 92R	44	91	35	1.800	2	$0.25 < P < 0.50$
	Total				11.133	10	$0.25 < P < 0.50$
	Pooled	124	268	118	1.467	2	$0.25 < P < 0.50$
	Heterogeneity				9.667	8	$0.25 < P < 0.50$

Table 2. Mean squares from analysis of variance of fatty acid concentrations in five BC_3F_2 populations segregating for the high-oleate trait.

Fatty acid	Recurrent parent	*Ol* genotype	Additive contrast	Dominance contrast	Parent × genotype	Parent × additive	Parent × dominance	Error
df	4	2	1	1	8	4	4	495
Palmitate (16:0), g kg^{-1}	3915**	15738**	28355**	491**	94*	125*	52	41
Stearate (18:0), g kg^{-1}	3761**	3	3	2	43	78	10	78
Oleate (18:1), g kg^{-1}	40590**	1018890**	1809530**	43241**	8515**	13810**	2575**	444
Linoleate (18:2), g kg^{-1}	42651**	809277**	1428175**	38572**	5493**	8586**	2010**	323
Total C_{18} species, g kg^{-1}	3568**	1244**	23039**	163	203**	310**	77	78
Arachidate (20:0), g kg^{-1}	275**	1	0	1	6	11	1	5
Gadoleate (20:1), g kg^{-1}	269**	205**	335**	24**	3	6*	1	2
Behenate (22:0), g kg^{-1}	580**	12	22	7	13	20	6	11
Lignocerate (24:0), g kg^{-1}	238**	6	10	1	5	11*	0	3
Total saturates, g kg^{-1}	241	15442**	28380**	270	387**	700**	45	150
O/L ratio (18:1/18:2)†	129**	10149**	11325**	5228**	58	89*	34	35

* Denotes means squares significant at $P \leq 0.05$.
** Denotes means squares significant at $P \leq 0.01$.
† Ratio of the concentration of oleate to linoleate.

under polygenic control. The separation of the effect of background genotype from that of the *ol* genes in this study suggests that the *ol* genes are not the only ones affecting fatty acid profiles in peanuts. It is also possible that there is polymorphism among the dominant alleles, Ol_1 and Ol_2, that might result in small differences among genotypes with "normal" fatty acid profiles. However, with sufficient resolution, multiple allelism for dominant *Ol* genes should result in observation of simple genetic ratios in progenies of crosses between low-oleate parents. This has not been the case in the published reports identified above.

As has been noted previously (Isleib et al., 1996), the *Ol* genotype influenced not only the concentrations of

Table 3. Genotypic means and estimates of genetic effects of the *ol* gene on fatty acid concentrations in five BC_3F_2 populations segregating for the high-oleate trait.

Fatty acid	Mean or contrast	Overall contrast	Contrast in NC 7	Contrast in NC 9	Contrast in NC 10C	Contrast in NC-V 11	Contrast in VA-C 92R
Palmitate (16:0)	Mean of *OlOl*	92.4 ± 1.0a†	83.4 ± 1.3a	102.7 ± 1.2a	93.5 ± 1.1a	93.4 ± 4.5a	89.1 ± 1.1a
	Mean of *Olol*	78.1 ± 0.5b	69.5 ± 0.8b	88.8 ± 1.0b	77.7 ± 0.9b	80.5 ± 1.7b	73.9 ± 0.7b
	Mean of *olol*	58.2 ± 0.8c	54.5 ± 1.2c	66.8 ± 1.3c	58.4 ± 1.3c	58.5 ± 3.2c	52.7 ± 1.0c
	Additive	17.1 ± 0.6**	14.4 ± 0.9**	18.0 ± 0.9**	17.6 ± 0.9**	17.5 ± 2.8**	18.2 ± 0.7**
	Dominance	2.8 ± 0.8**	0.5 ± 1.2	4.1 ± 1.4**	1.8 ± 1.2	4.6 ± 3.2	3.0 ± 1.0**
Oleate (18:1)	Mean of *OlOl*	527.2 ± 3.4c	576.8 ± 4.4c	482.7 ± 4.1c	535.7 ± 3.8c	518.4 ± 14.9c	522.3 ± 3.6c
	Mean of *Olol*	637.6 ± 1.6b	676.0 ± 2.6b	601.0 ± 3.4b	650.8 ± 2.8b	628.3 ± 5.6b	632.2 ± 2.2b
	Mean of *olol*	800.7 ± 2.6a	795.8 ± 3.9a	792.7 ± 4.3a	809.2 ± 4.4a	807.0 ± 10.5a	798.7 ± 3.2a
	Additive	−136.8 ± 2.1**	−109.5 ± 2.9**	−155.0 ± 3.0**	−136.8 ± 2.9**	−144.3 ± 9.1**	−138.2 ± 2.4**
	Dominance	−26.3 ± 2.7**	−10.3 ± 3.9**	−36.6 ± 4.5**	−21.7 ± 4.0**	−34.4 ± 10.7**	−28.3 ± 3.3**
Linoleate (18:2)	Mean of *OlOl*	280.4 ± 2.9a	235.9 ± 3.7a	323.9 ± 3.5a	272.4 ± 3.2a	285.7 ± 12.7a	284.3 ± 3.0a
	Mean of *Olol*	183.8 ± 1.3b	145.6 ± 2.2b	220.8 ± 2.9b	171.5 ± 2.4b	193.9 ± 4.8b	186.9 ± 1.9b
	Mean of *olol*	37.4 ± 2.3c	33.9 ± 3.3c	49.4 ± 3.7c	29.8 ± 3.7c	36.4 ± 9.0c	37.8 ± 2.7c
	Additive	121.5 ± 1.8**	101.0 ± 2.5**	137.2 ± 2.5**	121.3 ± 2.5**	124.7 ± 7.8**	123.3 ± 2.0**
	Dominance	24.8 ± 2.3**	10.7 ± 3.3**	34.1 ± 3.8**	20.4 ± 3.4**	32.9 ± 9.1**	25.9 ± 2.8**
Total C_{18} species	Mean of *OlOl*	849.7 ± 1.4c	857.4 ± 1.8c	838.9 ± 1.7c	856.4 ± 1.6c	848.9 ± 6.2c	847.0 ± 1.5c
	Mean of *Olol*	863.6 ± 0.7b	869.9 ± 1.1b	854.2 ± 1.4b	870.2 ± 1.2b	863.7 ± 2.4b	859.8 ± 0.9b
	Mean of *olol*	880.6 ± 1.1a	879.9 ± 1.6a	874.9 ± 1.8a	887.9 ± 1.8a	882.6 ± 4.4a	877.8 ± 1.3a
	Additive	−15.4 ± 0.9**	−11.2 ± 1.2**	−18.0 ± 1.2**	−15.8 ± 1.2**	−16.8 ± 3.8**	−15.4 ± 1.0**
	Dominance	−1.6 ± 1.1	1.2 ± 1.6	−2.7 ± 1.9	−2.0 ± 1.7	−2.0 ± 4.5	−2.6 ± 1.4
Gadoleate (20:1)	Mean of *OlOl*	9.8 ± 0.2c	9.7 ± 0.3c	11.1 ± 0.3c	7.5 ± 0.3c	10.0 ± 1.1b	10.8 ± 0.3c
	Mean of *Olol*	11.1 ± 0.1b	10.8 ± 0.2b	12.2 ± 0.2b	8.7 ± 0.2b	11.1 ± 0.4b	12.5 ± 0.2b
	Mean of *olol*	13.5 ± 0.2a	13.0 ± 0.3a	14.8 ± 0.3a	10.3 ± 0.3a	14.3 ± 0.7a	15.2 ± 0.2a
	Additive	−1.9 ± 0.2**	−1.6 ± 0.2**	−1.9 ± 0.2**	−1.4 ± 0.2**	−2.2 ± 0.6**	−2.2 ± 0.2**
	Dominance	−0.6 ± 0.2**	−0.5 ± 0.3	−0.8 ± 0.3*	−0.3 ± 0.3	−1.0 ± 0.8	−0.5 ± 0.2*
Lignocerate (24:0)	Mean of *OlOl*	10.2 ± 0.3a	9.1 ± 0.4b	11.5 ± 0.3a	8.3 ± 0.3a	10.7 ± 1.3a	11.4 ± 0.3c
	Mean of *Olol*	10.4 ± 0.1a	9.5 ± 0.2ab	11.3 ± 0.3a	8.5 ± 0.2a	10.6 ± 0.5a	12.2 ± 0.2b
	Mean of *olol*	10.9 ± 0.2a	10.2 ± 0.3a	11.0 ± 0.4a	8.7 ± 0.4a	11.4 ± 0.9a	13.1 ± 0.3a
	Additive	−0.3 ± 0.2	−0.5 ± 0.2*	0.3 ± 0.2	−0.2 ± 0.2	−0.3 ± 0.8	−0.8 ± 0.2**
	Dominance	−0.1 ± 0.2	−0.1 ± 0.3	0.1 ± 0.4	0.0 ± 0.3	−0.5 ± 0.9	−0.1 ± 0.3
Total saturates	Mean of *OlOl*	182.6 ± 2.0a	177.5 ± 2.6a	182.4 ± 2.4a	184.4 ± 2.2a	186.1 ± 8.7a	182.6 ± 2.1a
	Mean of *Olol*	167.6 ± 0.9b	167.6 ± 1.5b	166.0 ± 2.0b	169.1 ± 1.6b	166.7 ± 3.3b	168.4 ± 1.3b
	Mean of *olol*	148.3 ± 1.5c	157.3 ± 2.3c	143.1 ± 2.5c	150.7 ± 2.6c	142.4 ± 6.1c	148.3 ± 1.8c
	Additive	17.1 ± 1.2**	10.1 ± 1.7**	19.7 ± 1.7**	16.9 ± 1.7**	21.8 ± 5.3**	17.2 ± 1.4**
	Dominance	2.1 ± 1.5	0.2 ± 2.3	3.3 ± 2.6	1.5 ± 2.3	2.5 ± 6.2	2.9 ± 1.9
O/L ratio‡	Mean of *OlOl*	1.9 ± 0.9b	2.5 ± 1.2b	1.5 ± 1.1b	2.0 ± 1.1b	1.8 ± 4.2b	1.9 ± 1.0b
	Mean of *Olol*	3.6 ± 0.4b	4.7 ± 0.7b	2.7 ± 0.9b	3.9 ± 0.8b	3.3 ± 1.6b	3.4 ± 0.6b
	Mean of *olol*	23.6 ± 0.7a	24.6 ± 1.1a	21.0 ± 1.2a	27.9 ± 1.2a	22.6 ± 3.0a	21.8 ± 0.9a
	Additive	−10.8 ± 0.6**	−11.0 ± 0.8**	−9.8 ± 0.8**	−12.9 ± 0.8**	−10.4 ± 2.6**	−10.0 ± 0.7**
	Dominance	−9.1 ± 0.7**	−8.8 ± 1.1**	−8.5 ± 1.3**	−11.1 ± 1.1**	−8.9 ± 3.0**	−8.4 ± 0.9**

* Denotes means squares significant at $P \leq 0.05$.
** Denotes means squares significant at $P \leq 0.01$.
† a,b,c Means within a group of three followed by the same letter are not significantly different by *t* test ($P < 0.05$).
‡ Ratio of the concentration of oleate to linoleate.

oleate and linoleate in the populations ($P < 0.01$), but also the concentrations of palmitate, total C_{18} species, gadoleate, and total saturates, all at $P < 0.01$. This pleiotropic effect of the *ol* gene did not extend to all fatty acids: concentrations of stearate, arachidate, behenate, and lignocerate were not affected in spite of exhibiting genetic variation among the five populations. For each fatty acid influenced by the *ol* gene, the preponderance of the variation among *Ol* genotypes was attributable to its additive effect, dominance interaction accounting for as little as 0.7% of the total genotypic variation in total C_{18} species to 31.6% of the genotypic variation in O/L ratio. Dominance was statistically detectable averaged across all five background genotypes for concentrations of palmitate, oleate, linoleate, and gadoleate and for O/L ratio. Nonsignificance of the dominance contrast for traits with significant genotypic effects indicates gene action not detectably different from purely additive. This was the case for the concentrations of total C_{18} fatty acids and total saturates. Significance of the dominance contrast is indicative only of the presence of dominance, not its degree. Degree of dominance is best understood by comparing the relative magnitudes of the additive and dominance contrasts.

There was interaction between the effects of the *ol* gene and the background genotype of the population for concentrations of palmitate, oleate, linoleate, total C_{18} species, and total saturates (Table 2). The additive contrast interacted with background genotype for all those traits as well as gadoleate and lignocerate concentration and O/L ratio. Interaction between the dominance contrast and background genotype was significant ($P < 0.01$) only for oleate and linoleate concentration. If there were no interaction between the effects of the background genotype and the *ol* gene, then one could conclude that the genes producing the variation among recurrent parents were acting in an additive fashion with the *ol* gene to influence fatty acid composition. However, the significant interactions are indicative of nonadditivity of the effects of the various genes, that is, epistasis in the general sense. The discoverers of the high-oleate trait reported instances of digenic inheritance with duplicate gene action, resulting in a classical epistatic ratio in F_2 populations of certain crosses (Moore and Knauft, 1989; Knauft et al., 1993), but this is the first report of epistatic interactions other than between the named ol_1 and ol_2 loci.

The magnitudes and signs of the estimates of additive and dominance effects indicate partial dominance of the *Ol* allele for most of the fatty acids affected by the locus (Table 3). There was no dominance, that is, purely additive gene action, for total C_{18} species.

Results of the progeny test indicated that linoleate level in individual seeds was an accurate indicator of its *Ol-ol* genotype (Table 4). Of the 59 putatively heterozygous seeds that were progeny tested, 57 were found to be heterozygous while two were erroneously classified. This 96.6% success rate was significantly different from the 66.7% rate expected if the classification had been entirely random ($\chi^2 = 22.48$ with 1 df using Yates correction, $P < 0.001$). Likewise, 40 out of 41 putative *OlOl* homozygotes were correctly classified, a 97.6% success rate, significantly greater than the 33.3% expected if classification were random ($\chi^2 = 73.25$ with 1 df using Yates correction, $P < 0.001$).

Table 4. Results of progeny test of individual plants predicted to be heterozygous or homozygous (*OlOl*) on the basis of linoleate concentration in the planted seed.

	Predicted to be heterozygous (*Olol*)			Predicted to be homozygous (*OlOl*)		
Recurrent parent	Total	Correct	Incorrect	Total	Correct	Incorrect
NC 7	13	13	0	9	9	0
NC 9	10	8	2	10	10	0
NC 10C	12	12	0	10	10	0
NC-V 11	12	12	0	2	2	0
VA-C 92R	12	12	0	10	9	1
Total	59	57	2	41	40	1

These data show that the high-oleate trait is not completely recessive as previously reported. Because the normal oleate level exhibits incomplete dominance and heterozygotes can be identified with a high degree of accuracy, the transfer of the trait by backcrossing may be accomplished without imposing a selfing generation after making each backcross. Instead, the BC_iF_1 seeds with intermediate linoleate levels can be planted and used as parents for the BC_{i+1} cross.

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